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Seasonal variation in biomass and carbohydrate partitioning of understory sugar maple (*Acer saccharum*) and yellow birch (*Betula alleghaniensis*) seedlings

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Summary We investigated seasonal patterns of biomass and carbohydrate partitioning in relation to shoot growth phenology in two age classes of sugar maple (*Acer saccharum* Marsh.) and yellow birch (*Betula alleghaniensis* Britt.) seedlings growing in the understory of a partially harvested forest. The high root:shoot biomass ratio and carbohydrate concentration of sugar maple are characteristic of species with truncated growth patterns (i.e., cessation of aboveground shoot growth early in the growing season), a conservative growth strategy and high shade tolerance. The low root:shoot biomass ratio and carbohydrate concentration of yellow birch are characteristic of species with continuous growth patterns, an opportunistic growth strategy and low shade tolerance. In both species, starch represented up to 95% of total nonstructural carbohydrates and was mainly found in the roots. Contrary to our hypothesis, interspecific differences in shoot growth phenology (i.e., continuous versus truncated) did not result in differences in seasonal patterns of carbohydrate partitioning. Our results help explain the niche differentiation between sugar maple and yellow birch in temperate, deciduous understory forests.

Keywords: photosynthetic:non-photosynthetic tissue ratio, root:shoot ratio, starch, total nonstructural carbohydrates.

Introduction

Numerous studies have examined differences in shade tolerance among tree species. These studies have focused on interspecific variation in leaf morphology and physiology, photosynthetic responses, architectural adaptations, root:shoot ratio, biomass allocation patterns and the photosynthetic:non-photosynthetic tissue ratio (Boardman 1977, Givnish 1988, Lei and Lechowicz 1990, Ellsworth and Reich 1992, Walters et al. 1993*a*, 1993*b*, Bonser and Aarssen 1994, Naidu and DeLucia 1997*a*, 1997*b*, Kobe 1997, Beaudet and Messier 1998, DeLucia et al. 1998). Some studies have considered carbohydrate storage and have reported a trade-off between growth and carbohydrate storage which determines plant-level carbon allocation (Gholz and Cropper 1991).

There is substantial evidence that growth and maintenance respiration, defence and reserves represent competing carbon sinks in woody plants (Chapin et al. 1990, Kozlowski 1992). Because carbohydrate storage occurs when the carbon supply is greater than the carbon demand of growing and respiring tissues (Chapin et al. 1990), the storage allocation pattern is related to the growth pattern (Kozlowski and Keller 1966). Roots and lower stems generally accumulate carbohydrate reserves after cessation of aboveground growth (Dickson and Nelson 1982, Kays and Canham 1991). Many shade-tolerant species complete their aboveground shoot growth early in the growing season (Kozlowski and Ward 1957), whereas shade-intolerant species exhibit continuous shoot growth throughout the growing season (Walters and Reich 1999). Thus, shade-intolerant trees may maximize shoot elongation at the expense of allocation to carbohydrate reserves, thereby accumulating lower concentrations of carbohydrate reserves in the fall than shade-tolerant trees, which have a shorter period of shoot growth (Canham et al. 1999).

Acer saccharum Marsh. (sugar maple) and *Betula alleghaniensis* Britt. (yellow birch) are dominant species in the sugar maple–yellow birch forests of southern Québec (Robitaille and Majcen 1991). Baker (1949) and Logan (1970) considered yellow birch to be intermediate in shade tolerance. Yellow birch seedlings regenerate abundantly in canopy openings and after soil disturbance (Erdmann 1990). Yellow birch can achieve maximum height growth in environments ranging from 25 to 45% of full solar irradiance (Logan 1965). Sugar maple, in contrast, is considered highly shade tolerant (Baker 1949) and can persist for long periods under closed canopies (Hett and Loucks 1971). Sugar maple grows moderately well in low solar irradiance, but grows rapidly in response to canopy openings (Canham 1988, Ellsworth and Reich 1992). The species also differ in their seasonal patterns of shoot growth. Sugar maple growth is considered determinate or truncated because shoot elongation ends after full development of foliage

in mid-July (Kozlowski and Ward 1957), whereas yellow birch growth is continuous and shoot elongation may continue until leaf abscission (Kramer and Kozlowski 1979).

Sugar maple has a competitive advantage under closed canopy conditions, whereas yellow birch growth is favored in large gaps (Erdmann 1990). However, the dynamics of seedling regeneration and growth of these species after partial harvesting, when solar irradiation may permit the coexistence of several species, remain unpredictable. In addition, seedling age or size may influence the relationship between seedling growth rate and resource availability. Older seedlings usually have a more complex branching architecture than young seedlings, and invest more biomass in shoot and crown structure. It is unknown whether older or taller seedlings have a more efficient light harvesting strategy than younger seedlings.

In this study, we compared root:shoot ratios, photosynthetic:non-photosynthetic tissue ratio and carbohydrate allocation to various plant components in two age classes of sugar maple and yellow birch seedlings throughout an entire growng season. We hypothesized that (1) the seasonal pattern of carbohydrate partitioning is related to shoot growth phenology, (2) carbohydrates begin to accumulate in roots when shoot growth ends and (3) sugar maple allocates carbohydrates to roots earlier than yellow birch. To test these hypotheses, we: (1) characterized the seasonal patterns of growth and biomass partitioning in birch and maple seedlings; (2) examined how seasonal patterns of carbohydrate partitioning vary among the different types of carbohydrates (e.g., starches, metabolic sugars and minor sugars) within the various plant components and between tree species; and (3) compared biomass partitioning patterns for roots versus shoots and photosynthetic versus non-photosynthetic tissues, and overall carbohydrate concentrations in two age classes of seedlings.

Materials and methods

Study area

The study was conducted at two adjacent sites (each site was greater than 20 ha) in the Duchesnay Experimental Forest (46°55′ N, 71°40′ W), near Québec City, QC, Canada. Elevations in the study area range from 200 to 300 m, mean annual precipitation is 1200 mm and mean daily temperatures range from –12.8 °C in January to 18.3 °C in July (Environment Canada 1982). The soil is a Humo-Ferric Podzol on deep undifferentiated till deposits. Forests are dominated by sugar maple (*Acer saccharum*, 60%) in association with yellow birch (*Betula alleghaniensis*, 15%) and American beech (*Fagus grandifolia* J. F. Ehrh., 20%). White spruce (*Picea glauca* (Moench) Voss) and balsam fir (*Abies balsamea* (L.) Mill.) are occasionally present.

Sample collection

Samples were collected from two adjacent sites that had been partially harvested. Site 1 was harvested in the winter of 1988–1989 (88/89 site) and Site 2 was harvested in the winter of 1993–1994 (93/94 site), providing seedlings of different sizes and ages growing under similar light and soil conditions. Each site had similar canopy conditions, ranging from closed canopy to small gaps (100 m^2 in size). Irradiance ranged from 1 to 18% of above-canopy photosynthetic photon flux (PPF).

During the study, 300 seedlings were harvested for measurements of biomass and carbohydrate storage partitioning. Each harvest occurred within a 2-day period. Before harvesting, total height from root collar to terminal bud was measured in the field for each seedling. At each site and for each species, 15 seedlings were harvested in early November 1997 prior to winter dormancy, nine seedlings were harvested in early May 1998 just before bud flush, nine seedlings in early June 1998 after total bud flush, nine seedlings in early July 1998 after the end of crown development in sugar maple, nine seedlings in early August 1998 after the end of crown development in yellow birch, nine seedlings in mid-September 1998 just before leaf-fall, and 15 seedlings in mid-October 1998 at the beginning of winter dormancy. Harvested seedlings were sealed in plastic bags with wet soil around their roots to minimize water loss and stored at –4 °C until they were transported to the laboratory.

Light measurements

Light measurements were made between 0900 and 1600 h under overcast conditions as described by Parent and Messier (1996) and Gendron et al. (1998). Above-canopy PPF was measured with a point quantum sensor (LI-190SA, Li-Cor, Lincoln, NE) installed 3 m above ground in a large open area. This sensor was linked to a data logger (Li-Cor, LI-1000) that recorded 1-min means of readings taken every 5 s. Photosynthetic photon flux above each seedling was measured with a second point quantum sensor. The time of each measurement was recorded and the PPF above each seedling was calculated as a percentage of above-canopy PPF.

Biomass determination, root:shoot ratio and photosynthetic: non-photosynthetic tissue ratio

We divided seedlings into three components: (1) leaves or buds, depending on the harvest month, (2) stems and (3) roots. From May 1998 to October 1998, roots were separated further into fine (diameter < 2 mm) and large roots (diameter between 2 and 14 mm). Foliage, stems and roots were oven-dried at 60 °C for 1 week and dry biomass determined. Before drying, the stem base of each seedling was smoothed with sandpaper and the annual rings counted with the aid of a dissecting microscope to determine seedling age.

Root:shoot (R:S) and photosynthetic:non-photosynthetic tissue ratios (P:nP) were calculated from June to September 1998 as: R:S ratio = root biomass/(stem + leaf biomass) and P:nP ratio = leaf biomass/(stem + root biomass).

Extraction and quantification of soluble sugars and starch

Dried leaves, roots and shoots were ground separately with a Wiley mill (60 mesh). For stems and roots, a 100 mg subsample of ground plant tissue was extracted. Soluble sugars were extracted in 5 ml of 12:5:3 (v/v) methanol:chloroform: water (MCW). The extract was blended with a vortex and left

to settle for 10 min, then centrifuged at 1000 *g* for 10 min. The supernatant was removed and stored in a vial. The extraction procedure was repeated three times and all supernatants were combined. The pellet was saved for starch extraction. For leaves, we performed six extractions with 2.5 ml of MCW on a subsample of 50 mg of powder. We added 4.7 ml of water to the combined supernatants to separate them into two phases. The chloroform phase, which contained pigments, lipids and phospholipids, was discarded. The methanol–water phase was evaporated to dryness in a 55 °C oven and redissolved in 2 ml of water. Samples were stored at –80 °C for soluble sugar determination.

Starch contained in the pellet remaining after the extraction of soluble sugars was hydrolyzed to glucose (Haissig and Dickson 1979). The pellet was oven-dried for 8–10 h at 55 °C and hydrolyzed at 57 °C for 3 h with 7 ml of enzymatic solution containing 2 ml of amyloglucosidase (150 enzymatic units ml^{-1} in citrate buffer, pH 4.6; Sigma, St. Louis, MO). Extracts were centrifuged at 5000 *g* for 10 min. The supernatant was retained and stored at –80 °C for starch quantification.

Glucose contents of the starch hydrolysates and the individual soluble sugars were determined by high performance liquid chromatography (HPLC) with a refractive index detector (model 410, Waters, Milford, MA). We used a heated (90 °C) cation-exchange column with strong cationic support (Ca) (Sugar pak 1, Waters), H_2O-EDTA (50 mg l^{-1}) as aqueous mobile phase, and a flow rate of 0.5 ml min^{-1} for soluble sugars and 0.6 ml min^{-1} for starch hydrolysates. Before injection into the refractive index detector, all samples were clarified on C-18 Sep-paks (Millipore) and filtered (0.45-µm mesh) to remove impurities. The injection volume was 20 µl. Peak identities and sugar quantities were determined by comparison with standards. Nine peaks were observed, but only seven identified; their elution times (in min) were: sucrose 7.03, glucose 8.68, galactose 9.48, fructose 10.06, mannitol 11.42, sorbitol 13.08 and ribose 14.22. Sugar concentrations were calculated from standard curves.

Carbohydrate analysis

Carbohydrates were divided by physiological function into three classes: starch, metabolic sugars (sucrose, glucose and fructose) and other minor carbohydrates (galactose, mannitol, sorbitol and ribose). The concentration of total nonstructural carbohydrates (TNC) for the whole plant was calculated as: $C_{total} = (C_L DM_L + C_S DM_S + C_R DM_R)/(DM_L + DM_S + DM_R)$, where C = TNC concentration (mg g^{-1}), DM = total dry mass (g) and L, S and R = leaves, stem and roots, respectively. We calculated the concentration of each carbohydrate class in leaves, stems, fine roots and large roots of seedlings.

Statistical analysis

Differences in mean seedling height and age between species and sites were subjected to analysis of variance (ANOVA) to ensure that seedling heights and ages were similar within sites and between species. Hereafter, the differences found between younger and smaller seedlings at the 93/94 site and older and taller seedlings at the 88/89 site are referred to as age effects.

Effects of species (birch and maple), seedling age (93/94 and 88/89 sites) and their species × age interactions on root:shoot ratios, photosynthetic:non-photosynthetic tissue ratios and carbohydrate concentrations were tested by two-way ANOVA. We also used ANOVA to test the effects of species, age and month of sampling on the same parameters. When assumptions of normality and homogeneity of variance were unmet, root:shoot ratio, photosynthetic:non-photosynthetic tissue ratio or carbohydrate concentrations were classified into ranks and ANOVAs were rerun. All P values = 0.05 were considered significant. Statistical analyses were performed with JMPin 3.2.1 software (SAS Institute, Cary, NC).

Results

Seedling height and age

Seedlings from the 93/94 site were younger and smaller than seedings from the 88/89 site ($P = 0.0001$). In the study year, sugar maple seedlings were 9 ± 4 years old and yellow birch seedlings were 8 ± 1 years old at the 88/89 site, and the corresponding ages for the 93/94 site were 5 ± 1 and 4 ± 1 years (± SE, $n = 75$ for each species at each site). Mean shoot lengths of sugar maple and yellow birch at the 93/94 site were 37 ± 1 and 52 ± 2 cm, respectively, and the corresponding values at the 88/89 site were 78 ± 4 and 90 ± 5 cm.

Biomass partitioning

Mean root:shoot ratios varied significantly between species (based on values from June to September 1998, Table 1). Yellow birch seedlings allocated more biomass to above- than belowground tissues (70 versus 30% of dry mass), whereas sugar maple seedlings had similar above- and belowground biomass (55 versus 45% of dry mass). We found no difference in root:shoot ratios between 4- and 8-year-old birches; however, older maple seedlings had higher shoot allocation than younger maple seedlings (Table 1).

Allocation to photosynthetic and non-photosynthetic tissues varied significantly with seedling age but not with species (Table 1). In both species, higher allocation to photosynthetic tissues was found in younger seedlings. Allocation to photosynthetic tissues represented 25% of the total biomass of the seedlings from the 93/94 site, whereas it represented 15% of the total biomass of the seedlings from the 88/89 site (Table 1).

Biomass partitioning as a function of shoot growth phenology

Biomass partitioning varied significantly during the growing season for young seedlings of both species ($P = 0.002$ and $P = 0.01$ for birch and maple seedlings, respectively, Figure 1A). Young seedlings had significantly greater root biomass in early July than in other months of the growing season. In older seedlings, allocation to root versus shoot tissues did not vary significantly during the growing season, although there was a near-significant trend ($P = 0.06$) for older maple seedlings to have greater root biomass in September than in other months.

Table 1. Root:shoot biomass (R:S) and photosynthetic:non-photosynthetic (P:nP) tissue biomass ratios (means ± SE) of yellow birch and sugar maple seedlings according to site of sampling. Analyses were performed on June, July, August and September 1998 data. Different letters (x, y) within a species indicate significant differences at $P = 0.05$. The P values are given by two-way ANOVAs.

Site	R:S ratio	P:nP ratio
Yellow birch		
88/89	0.44 ± 0.02	0.16 ± 0.02 x
93/94	0.46 ± 0.03	0.38 ± 0.03 y
Sugar maple		
88/99	0.72 ± 0.05 x	0.17 ± 0.01 x
93/94	0.89 ± 0.05 y	0.30 ± 0.03 y
	P value	
Species	< 0.0001	0.121
Site	0.006	< 0.0001
Species × site	0.200	0.061

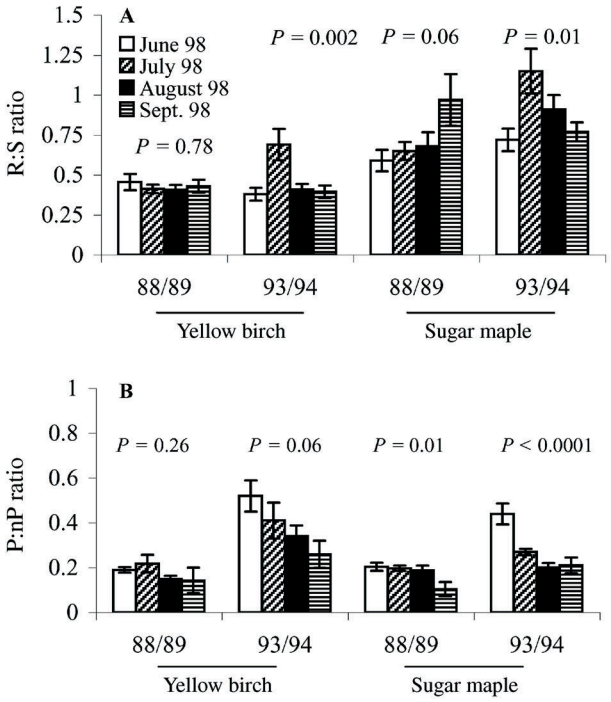

Figure 1. Seasonal patterns in (A) root:shoot biomass (R:S) and (B) photosynthetic:non-photosynthetic (P:nP) tissue biomass ratios of sugar maple and yellow birch seedlings at each study site (88/89 and 93/94 harvested sites). Values represent means ± 1 SE.

Allocation to photosynthetic tissues in young maple seedlings was significantly higher in early June than at other times of the growing season ($P < 0.0001$) (Figure 1B). At this time, leaves were fully developed and represented a large percentage of the total biomass of the young seedlings. Young birch seedlings showed a decrease in P:nP ratio from early June to mid-September ($P = 0.06$). Allocation to photosynthetic tissues ended earlier in the growing season in young sugar maple seedlings than in young birches. In older sugar maple seedlings, allocation to non-photosynthetic tissues was greater in mid-September than during earlier months ($P = 0.01$), whereas no significant difference was found for older birch seedlings.

Carbohydrate concentration and seasonal carbohydrate allocation

Total nonstructural carbohydrates in seedlings comprised mostly starches (93–95%) and small amounts of metabolic sugars (4–5% sucrose, glucose and fructose) and other minor sugars (1–2% galactose, mannitol, sorbitol and ribose) (Table 2). Carbohydrate reserves (i.e., TNC) and starch concentrations were 1.3 to 2 times higher in maple seedlings than in birch seedlings of both ages. Although seedling age had a significant effect on concentrations of TNC, starch and other sugars, only maple seedlings showed declines in the concentrations of these carbohydrates with age (Table 2).

Because seasonal variations in carbohydrate concentrations were similar for young and old seedlings (data not shown), the data were pooled for further analyses. Results of two-way ANOVAs showed that sugar maple seedlings had higher TNC concentrations than birch seedlings from early May to mid-October for whole seedlings ($P < 0.0001$), stems ($P = 0.02$), fine roots ($P = 0.04$) and large roots ($P < 0.0001$). In contrast, the two species had similar foliar concentrations of TNC (Figure 2). Carbohydrate reserves varied significantly during the growing season for whole seedlings, stems, fine roots and large roots ($P < 0.0001$), but not for leaves. There was a significant interaction between species and sampling month for stems ($P = 0.049$) and fine roots ($P = 0.008$) (Figure 2), caused by a trend reversal in September.

Carbohydrate reserves in maple stems were greatest in early July, whereas reserves in birch stems were high in early July and again in September–October (Figure 2A). Concentrations of TNC were similar in maple and birch leaves and did not change from early June to mid-September (Figure 2B). In autumn, carbohydrate reserves were greatest in mid-September for both maple and birch fine roots (Figure 2C). In large roots of both maple and birch, carbohydrate reserves accumulated in mid-September after depletion in early August, and then decreased again in mid-October (Figure 2D). Whole-plant carbohydrate reserves were greatest in September–October for maple, whereas birch seedlings showed an increase in mid-September followed by a sharp decrease in mid-October (Figure 2E).

Total starch content was greater in sugar maple seedlings than in birch seedlings ($P < 0.0001$), and seasonal differences were significant ($P < 0.0001$) in both species (Figure 3A). In general, seasonal variation in starch concentrations closely mirrored patterns in TNC concentrations. Starch concentrations were highest in mid-September and mid-October in sugar maple, whereas yellow birch had high concentrations in mid-September followed by a decrease in mid-October (Figure 3A). The species had similar concentrations of metabolic sugars, with high concentrations in early June. Birch seedlings had significantly higher concentrations of metabolic sugars at

Table 2. Concentrations of total nonstructural carbohydrates (TNC), starch, metabolic sugars (sucrose + glucose + fructose) and other sugars (galactose + mannitol + sorbitol + ribose) (means ± SE) in whole yellow birch and sugar maple seedlings according to site. Analyses were performed on June, July, August and September 1998 data. Different letters (a, b) within the same site indicate significant difference between species at $P = 0.05$. Different letters (x, y) within the same species indicate significant difference between sites at $P = 0.05$. The P values are given by two-way ANOVA. Sites 1 and 2 were harvested in 1988/89 and 1993/94, respectively. Abbreviation: ns = non-significant.

Species	Site	Concentration (mg g_{DM}^{-1})			
		TNC	Starch	Metabolic sugars	Other sugars
Yellow birch	Site 1	31.21 ± 3.35 a	29.27 ± 3.31 a	1.47 ± 0.14	0.47 ± 0.04
	Site 2	32.90 ± 4.65 a	30.49 ± 4.66 a	1.72 ± 0.16	0.70 ± 0.11
Sugar maple	Site 1	42.77 ± 3.55 b, x	40.30 ± 3.50 b, x	1.83 ± .021	0.64 ± 0.09 x
	Site 2	66.50 ± 4.68 b, y	63.35 ± 4.77 b, y	2.39 ± 0.51	0.76 ± 0.05 y
		P value			
Species		< 0.0001	< 0.0001	ns	ns
Site		0.002	0.003	ns	0.033
Species × site		0.008	0.009	ns	ns

the end of growing season compared with early in the growing season (Figure 3B). Concentrations of other minor sugars were higher in maple seedlings than in birch seedlings and showed a peak in mid-October after some depletion in early August in both species (Figure 3C).

Discussion

Interspecific differences in growth patterns

Several studies have shown that seasonal growth patterns are related to growth strategy and that different growth strategies lead to different degrees of shade tolerance (Kobe et al. 1995, Kobe and Coates 1997, Canham et al. 1999). The differences in biomass partitioning patterns that we observed between sugar maple and yellow birch seedlings reflected differences in shoot growth patterns and shade tolerance. Maple seedlings showed responses characteristic of shade-tolerant species with truncated growth patterns (i.e., cessation of aboveground shoot growth early in the growing season), and yellow birch seedlings exhibited biomass partitioning patterns characteristic of shade-intolerant species with continuous growth patterns (i.e., a continuous extension of stems and leaves throughout the growing season) (cf. Logan 1965, Walters et al. 1993*a*, 1993*b*).

Carbohydrate reserves distribution among plant parts

Carbohydrates were present in leaves, stems and large and fine roots of both species. Starch and TNC concentrations in stems and roots of sugar maple were consistent with those found in the literature for sugar maple and other birch species, whereas soluble sugar concentrations of maple were lower than those reported previously (Wargo 1979, Gregory and Wargo 1985, Renaud and Mauffette 1989, 1991). In both yellow birch and sugar maple seedlings, starch represented up to 95% of the TNC and was found mainly in the roots. We found greater starch concentrations in large roots than in fine roots, presumably because large roots can serve as storage organs, whereas the role of fine roots is to absorb water (Gholz and Cropper 1991). Leaves of both species contained high concentrations of starch. Starch is accumulated in chloroplasts during the day and is broken down to soluble sugars during the night and reallocated to stems and roots (Chapin et al. 1990, Kobe 1997).

Interspecific differences in carbohydrate concentrations

We found no difference in concentrations of metabolic and other sugars between sugar maple and yellow birch seedlings, whereas TNC and starch content were 1.3 to 2 times higher in maple than in birch from May to October. Yellow birch allocated most of its newly synthesized carbohydrate to stem extension and to emerging leaves, reflecting the opportunistic growth strategy of birch seedlings which depends on high carbon assimilation rates, even at low irradiances, to maintain rapid growth. As a result, compared with sugar maple, fewer carbohydrates were allocated to root starch reserves. The conservative (or survivalist) strategy of slow-growing sugar maple was associated with the allocation of a large fraction of biomass to belowground tissues and the accumulation of large carbohydrate reserves in roots. Walters et al. (1993*a*) suggested that higher allocation to roots than to shoots occurs at the expense of rapid growth rates, but favors long-term survival under persistent shade. This is consistent with our results showing slower height growth in sugar maple than in birch. Slower height growth may also reflect the relatively low assimilation rates reported for sugar maple seedlings (Niinemets and Tenhunen 1997, Gaucher et al. 2003).

The accumulation of carbohydrate reserves is part of the survival strategy of shade-tolerant species. A strong relationship between carbohydrate reserves in roots and survival in deciduous and evergreen tree species has been reported previously (Kobe 1997, Canham et al. 1999). High TNC concentrations have been shown to play an important role in recovery of seedlings following disturbance, stress, damage and winter hardening, as well as in protection from pathogens and insect

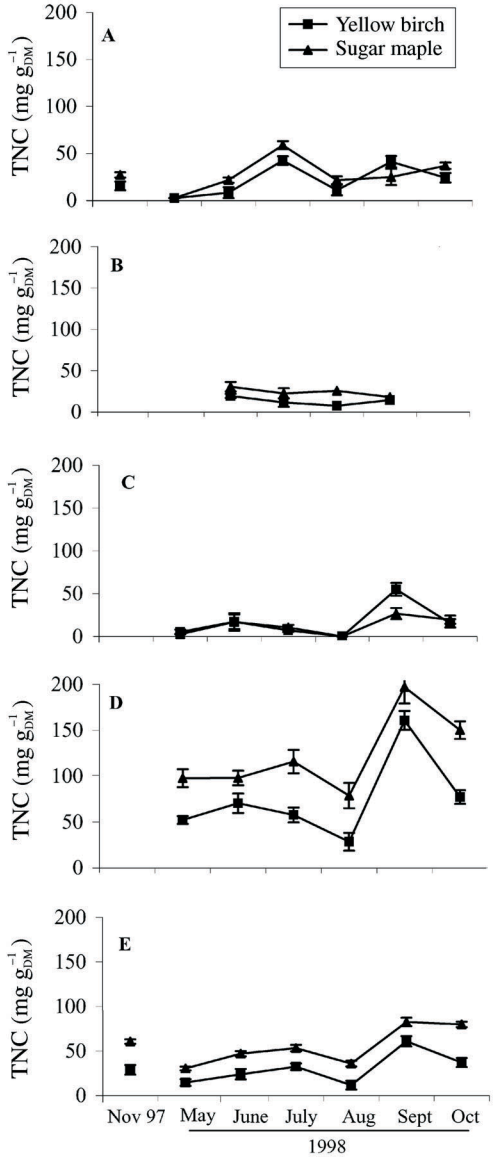

Figure 2. Seasonal variation in total nonstructural carbohydrates (TNC) concentrations in (A) stems, (B) leaves, (C) fine roots, (D) large roots and (E) whole seedlings of sugar maple and yellow birch. Values represent means ± 1 SE.

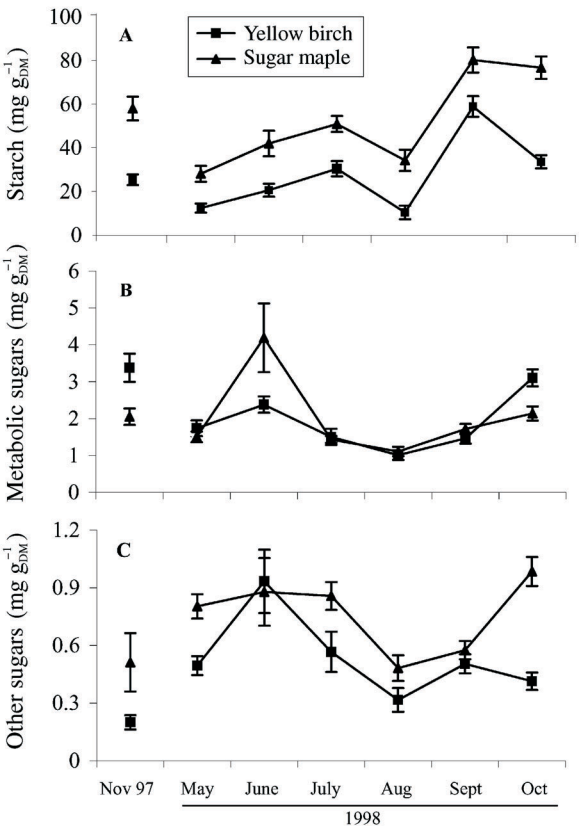

Figure 3. Seasonal variation in carbohydrate concentrations in sugar maple and yellow birch seedlings: (A) starch, (B) metabolic sugars (sucrose + glucose + fructose) and (C) other sugars (galactose + mannitol + sorbitol + ribose). Values represent means ± 1 SE.

attack (Chapin et al. 1990, Renaud and Mauffette 1991, Liu and Tyree 1997, Liu et al. 1997).

Photosynthetic:non-photosynthetic tissue and root:shoot ratios, carbohydrate reserves and seedling age

In sugar maple, branching is generally not initiated until seedlings are 4 to 6 years old because of strong apical dominance (Bonser and Aarssen 1994). The onset of branching may explain the higher P:nP and R:S ratios in young (5 ± 1 years old) than in old (9 ± 4 years old) maple seedlings. In old seedlings, stems represented a larger percentage of total plant biomass, resulting in a larger shoot biomass and larger biomass of non-photosynthetic tissues. Our results are consistent with those of Messier and Nikinmaa (2000), who reported a large decrease in leaf area ratio (photosynthetic tissues) with increasing stem height up to 1.5 m for sugar maple and yellow birch seedlings. Furthermore, older and larger seedlings generally allocate more carbon to the maintenance and construction of stems and roots (Givnish 1988), which may explain the smaller pool of carbohydrate reserves in older maple sugar seedlings compared with young seedlings. For yellow birch, the P:nP ratio decreased with increasing age, whereas the R:S ratio did not, reflecting the rapid growth of this species.

Seasonal variation in carbohydrate allocation and reserves

Seasonal variations in carbohydrate reserves and starch concentrations in all plant components were similar for yellow birch and sugar maple seedlings throughout the growing season. Concentrations of TNC and starch in large roots of both species were constant from May to July, peaked in mid-September before leaf abscission and then decreased in mid-October (except starch concentrations in sugar maple). It has been shown that the breakdown of starch reserves in roots occurs at the beginning of winter dormancy (Wargo 1979), and the resulting soluble sugars are allocated to root elongation and maintenance of the belowground system (Kozlowski 1971).

Soluble sugars may also play a role in winter hardening by acting as cryoprotectants (Tinus et al. 2000). Based on these studies, we attribute the increase in concentrations of metabolic and minor sugars in yellow birch in October to the conversion of starch to soluble sugars.

In August, we observed a slight decline in whole-seedling carbohydrate concentration that may have been caused by a mild drought that occurred in late July (Environment Canada, http://www.climat.meteo.ec.gc.ca). Other studies have reported that, in response to mild water deficiency, starch is converted to soluble sugars to provide energy for the increased metabolic cost associated with drought stress, maintain turgor pressure and support growth of new roots (Friend et al. 1991).

In older birch seedlings, the R:S ratio was constant during the growing season; however, young birch seedlings showed an increase in R:S ratio and a high accumulation of TNC in shoots in early July. This may be explained by episodic flushes of growth in young birch seedlings that temporarily accumulate carbohydrates between flushes. Alternatively, it may be that photosynthesis in the young birch seedlings did not attain maximum photosynthetic capacity under the light conditions of the experiment (1–18% of above-canopy PPF), and were therefore unable to grow continuously between June and early July.

We hypothesized that birch, with a continuous growth pattern, would allocate carbohydrates to roots later in the growing season than maple seedlings with a truncated growth pattern. However, birch and maple seedlings had similar seasonal patterns of carbohydrate allocation. This similarity may be associated with the relatively low irradiances in the study area that did not support growth of yellow birch seedlings in the fall. As a result, in both species, photosynthates were allocated to carbohydrate reserves in the fall. Maple seedlings showed strategies for long-term survival under the relatively low light conditions by allocating a large fraction of biomass to belowground tissues and accumulating large carbohydrate reserves in roots.

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